

LENGTH-WEIGHT RELATIONSHIPS OF JAMAICAN ARTHROPODS¹

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ABSTRACT: We calculated length-weight regressions for above ground and leaf litter arthropods collected in Jamaica. Slope coefficients were generally lower (suggesting thinner, lighter bodies) than those reported from drier temperate regions, but were similar to those reported from moist Costa Rica for all taxa except Homoptera. This result is consistent with the hypothesis that selection has favored elongated body shapes in wet tropical regions where arthropods are little constrained by desiccation. The low slope for Jamaican Homoptera may be because small thin-bodied families (Cixiidae, Psyllidae, and Aphididae) are disproportionately more common in Caribbean than Central American insect faunas. Within Jamaica, slopes were lower for arthropods collected in wet habitats (wet limestone forest, mangrove swamp) than dry habitats (dry limestone forest, coastal thorn scrub), further suggesting the importance of microclimate as a factor influencing arthropod shape. However, leaf litter arthropods, which are relatively protected from desiccation, had higher slopes than those collected above ground, suggesting that other constraints, perhaps those imposed by means of locomotion, also affect arthropod shape.

Estimating the biomass of arthropods is important in biological studies due to the great abundance of arthropods in most ecological communities (Sample et al. 1993), their importance as a vertebrate food resource (Golley 1961), and their role as model organisms to study evolutionary processes affecting morphology (Schoener and Janzen 1968, Schoener 1980). In this regard, length-weight regressions have provided useful tools in estimating arthropod biomass in particular habitats (Rogers et al. 1977, Pearson and Derr 1986), examining the biomass of particular prey size classes in consumer diets (Harris 1986, Torok and Ludvig 1988, Omland and Sherry 1994), describing predator foraging behaviors (Sage 1982, Hill and Grossman 1993, Pulido and Diaz 1997), and comparing morphologies of insects in different regions (Schoener 1980). Comparative studies have found that due to differences in general arthropod shape, the coefficients of length-weight regressions can vary significantly between taxa (Rogers et al. 1977), and within taxa between regions (Schoener 1980). Thus, accurate regressions are best computed from locally collected specimens for as many different taxa as feasible (Rogers et al. 1976; Sample et al. 1993; Hodar 1996). To date, relatively few length-weight regressions are available for tropical arthropods (Schoener 1980), and no regressions have been reported for Caribbean islands.

The few data available suggest that tropical arthropods tend to be rela-

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tively long and thin (lower regression slope coefficients) compared to their temperate counterparts (Schoener 1980). In offering an explanation for this pattern, Schoener (1980) suggested that climatic factors may be important. He reasoned that in arid regions, insects may be constrained to minimize surface area to volume ratios to counter desiccation. Therefore, selection pressure would favor (in addition to larger sizes) arthropods with more compact shapes (i.e., more spherical or cubic) with higher slope coefficients (i.e., closer to 3, *sensu* McMahon 1973). Conversely, in wet regions such as the tropics, arthropods would be relatively free from this constraint, and other selection pressures, such as risk of predation, may favor more elongated, cryptic body shapes. In support of this hypothesis, Schoener (1980) found that insects collected from wet forests in Costa Rica had lower slopes than those collected from drier sites, but other comparative data are lacking.

In this study, we present the first length-weight regressions of arthropods from Jamaica. In addition, we test the hypothesis that selection has favored elongated body shapes in wet areas where arthropods are little constrained by desiccation by testing predictions at three spatial scales. First, we predict regression slopes derived from our Jamaican collections to be lower than those obtained from insects in drier temperate regions, but similar to those from other tropical areas. Second, among our Jamaican samples, we predict the slopes of insects collected in relatively wet habitats (mangrove swamp and wet limestone forests) to be lower than those derived from insects collected in drier habitats (dry limestone forest and thorn scrub). Third, we predict that leaf litter arthropods are less constrained by desiccation than above ground arthropods, and consequently will yield lower length-weight regression slopes than arthropods collected above ground (i.e., foliage-dwelling and free-flying species).

METHODS

We collected arthropods using several techniques: branch clipping and Malaise trapping for above ground arthropods, and Berlese funnels and spot collecting for leaf litter arthropods. Branch clipping (Johnson 2000) consisted of positioning a collapsible bag in the understory or canopy (up to 9 m with the aid of extension poles), quickly enclosing the end of a branch, tightening the mouth of the bag around the branch with a drawstring, clipping the branch free with a telescoping tree pruner, then lowering the bag and visually inspecting the clipped branch for arthropods. Arthropod specimens were collected from the bag with an aspirator, and stored in 70% ethanol. Malaise trapping was conducted with standard Malaise traps (2 m high, pyramidal construction, Bioquip Inc., Cooper and Whitmore, 1990), which were erected and operated for approximately 24 hr. Lepidopteran adults were presorted from the collections in the field and stored in plasticine envelopes; other arthropods were stored in 70% ethanol.

To collect leaf litter arthropods, we pushed a 0.1 m² cylindrical core into the subsoil, collected all leaves and leaf fragments and briefly stored them in plastic bags. The leaves and leaf fragments were then placed in Berlese funnels for 14 h and the extracted arthropods were stored in 70% ethanol (see Levings and Windsor 1982 for additional details). A few additional specimens were collected with forceps directly from the leaf litter.

All sampling was conducted in the dry season (Nov. - Mar.) 1995-1997, except for above ground Aranae, which were collected in June 1998. We collected specimens from 26 sites representing six broad habitats along a wet-dry gradient (Fig. 1, Table 1). A habitat's moisture is a complex interaction of rainfall, temperature, evapotranspiration rates, and local shade conditions, and different sites within a habitat are not equivalent. Thus, rather than quantifying this wet-dry gradient, we instead ranked these six habitats based on patterns of rainfall and our own experience working in each of the sites (listed in order of increasing aridity): wet limestone forest, mangrove swamp, citrus orchard, shade-coffee plantation, dry limestone forest, and coastal thorn scrub. Habitat descriptions, including dominant plant species, are available in Asprey and Robbins (1953); more detailed site descriptions are available in Johnson (1999). For purposes of this report, arthropods from all habitats were pooled to provide adequate sample sizes to generate order-specific length-weight regressions which serve as general relationships for the island. To compare regression coefficients between habitats, we pooled all insect orders within a habitat to maintain adequate sample sizes. Regressions were run separately for above ground and leaf litter arthropods.

In the laboratory, all above ground adult arthropods were sorted into 12 taxonomic groups corresponding closely to order: Aranae, Orthoptera, Dictyoptera, Hemiptera, Homoptera, Coleoptera, Lepidoptera, Nematocera, other Diptera, Formicidae, and other Hymenoptera. Leaf litter arthropods were sorted into 10 groups: Aranae, Pseudoscorpiones, "Arthropods" (Diplopoda, Chilopoda, and Isopoda), Dictyoptera, Isoptera, Dermaptera, Hemiptera, Coleoptera, Formicidae, and various holometabolous larvae (Coleoptera, Lepidoptera, and Diptera). The lengths of all arthropods were measured (head to end of abdomen) to the nearest 0.1 mm using a 7.5-64x dissecting microscope equipped with an ocular micrometer, dried to constant mass (24 hr at 100° C), allowed to cool, and weighed to the nearest 0.1 mg using an electronic balance. To avoid pseudoreplication, we included multiple specimens of the same morphospecies only when they were of different lengths (with the exception of Isoptera, in which variation in length was slight). Small specimens (<1.5 mm), when weighed singly, resulted in only 1 significant digit for mass with a 0.1 mg precision balance. Therefore, wherever possible we weighed 2-10 small individuals of the same length and morphospecies together, then calculated a mean weight.

We used the power model described by Rogers et al. (1977) to calculate length-weight regressions of arthropod taxa with the formula:

$$\text{Weight} = b_0 (\text{length})^{b_1}$$

where b_0 and b_1 are constants. This equation was transformed with natural logarithms to

$$\ln(\text{weight}) = \ln(b_0) + b_1 \ln(\text{length})$$

and expressed in linear form for regression ($Y = B_0 + B_1X$) so that an arthropod's estimated weight may be calculated from its length and the regression coefficients using the formula:

$$\text{Weight in mg} = e^{B_0} (\text{length in mm})^{B_1}$$

where $B_0 = \ln(b_0)$ and $B_1 = b_1$, corresponding to the y-intercept and slope of the regression line respectively. Regression coefficients were calculated using SYSTAT 5.2.1 (Wilkinson 1989) and Excel 5.0 (Microsoft 1994). We compared slopes of Jamaican arthropods collected in different habitats with a test of homogeneity of slopes (THS, Sokal and Rohlf 1981). Strict statistical comparisons of slope (power) coefficients with previously published results are impossible without all the data used to generate the coefficients, thus, we compared slopes qualitatively and by examining confidence intervals (Sokal and Rohlf 1981).

RESULTS AND DISCUSSION

All length-weight regressions were statistically significant ($P < 0.01$) and correlation coefficients were generally high (r range 0.574-0.979, Tables 2 and 3). Low slope coefficients (B_1) indicate groups that are relatively light for their length, as is the case for thin, slight-bodied arthropods. Among Jamaican above ground arthropods (Table 2), slopes were lowest for Nematocera, other Diptera, and Homoptera (1.317-1.876) and highest for Hemiptera, Lepidoptera, and Dictyoptera (2.219-2.311). Slopes were lowest among leaf litter fauna for "arthropods" (Diplopoda, Chilopoda, and Isopoda, 2.014) and highest for Isoptera (3.177, Table 3). Regressions of morphologically diverse taxa for which we had many specimens, such as Coleoptera and Hemiptera (the latter included Emesinae [thread-legged bugs] and Pentatomidae [stink bugs]), yielded correlation coefficients that were as high as those found in morphologically stereotyped taxa for which specimens were uncommon (e.g., Nematocera, above ground Formicidae). This suggests that sample size, as much as morphological diversity, contributes to the variation in the precision of length-weight correlations.

To examine the effect of regional climate on arthropod shape, we compared regression slope coefficients derived from our Jamaican specimens with those previously published from temperate areas (Rogers et al. 1977, Sample et al. 1993) and from other tropical regions (Schoener 1980). Overall, the slopes calculated in this study were lower (all < 2.79 except for Isoptera) than those calculated from insects in temperate regions, which usually have values between 2.60 and 3.30, corroborating the pattern first documented by Schoener (1980). Comparing slopes within the tropics (only data from above ground insects were available), Jamaican slopes were, with one notable exception, similar to those for insects from Costa Rica (Schoener 1980). All 95% confidence intervals from Jamaican regressions, except those for Homoptera, contained the power coefficients of the corresponding taxa from either wet or dry habitats in Costa Rica (Table 4). These results support the hypothesis that selection has favored elongated body shapes in the wet tropics.

The particularly low slope of Jamaican Homoptera may be due to adaptations for camouflage. Within Homoptera, small phytophagous groups (such as Cixiidae, Psyllidae, and Aphididae) are disproportionately more abundant on Caribbean islands than on the Central American mainland (Janzen 1973). These groups, which can be important prey for Caribbean birds (Lack 1972), may be under especially intense selective pressure to blend in with their surroundings, and a thin shape has been suggested to be an advantage for camouflage (Schoener 1980). In support of this, Sample et al. (1993) found the slope of Cixiidae to be lower than that for other Homopterans. Thus, a high relative proportion of small, thin, camouflaged families within Homoptera on Caribbean islands may tend to keep the regression slope low relative to regions where Homopteran morphologies are more diverse.

To further evaluate the hypothesis that climate affects arthropod shape, we examined the slope coefficients derived from Jamaican above ground specimens collected in habitats across a wet-dry gradient. Leaf litter arthropods could not be analyzed separately by habitat because collections had been previously pooled across habitats for other analyses (Strong and Sherry in press). A test for the homogeneity of slopes demonstrated that arthropods collected in the six habitats resulted in significantly different slopes ($P < 0.01$, Fig. 2). As predicted, the wetter habitats (wet limestone forest and mangrove swamp) had the lowest slopes, whereas the more arid habitats (dry limestone forest and coastal thorn scrub) contained the highest slopes.

Lastly, we compared the slopes of leaf litter arthropods, which may be buffered somewhat from desiccation, to those from above ground specimens. In taxa for which we had adequate sample sizes (Araneae, Dictyoptera; Hemiptera, Coleoptera, and Formicidae), the slopes of Jamaican above ground arthropods were lower than those for leaf litter arthropods (Tables 2 and 3), indicating longer thinner arthropods above the ground, where desiccation risk is higher. This result is inconsistent with the hypothesis that microclimate is

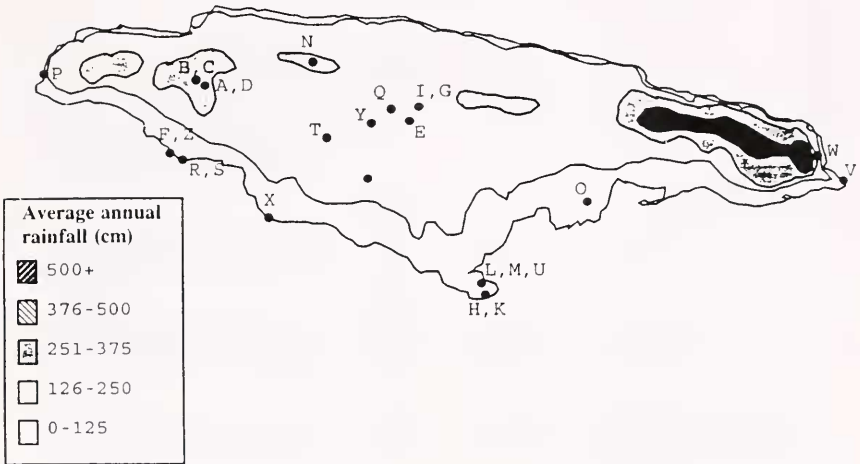


Fig. 1. Collection sites and average annual rainfall in Jamaica (data from Lack 1976). See Table 1 for list of collection sites.

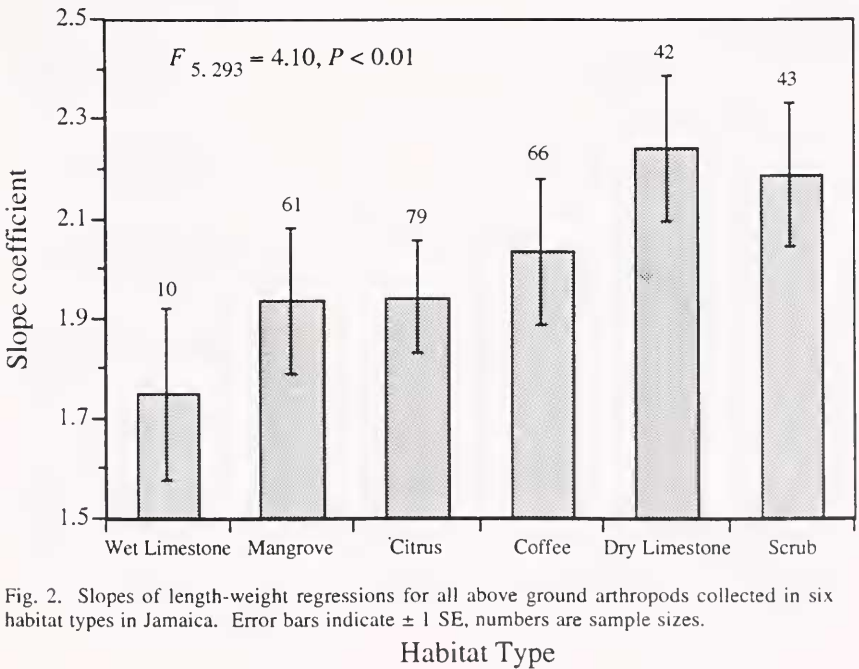


Fig. 2. Slopes of length-weight regressions for all above ground arthropods collected in six habitat types in Jamaica. Error bars indicate ± 1 SE, numbers are sample sizes.

Table 1. Study sites lettered by collection date, sorted by broad habitat types.

Study Site	Habitat Type	Lat.- Long.	Elevation Range	Site Description
A. Copse Mountain	Wet Limestone Forest	18°16'N 77°04'W	440-460 m	Tall, dense, old-aged wet forest fragment with several hurricane-formed gaps containing thick understories and vines
J. Marshall's Pen	Wet Limestone Forest	18°03'N 77°32'W	600-620 m	Second growth moist forest fragment with continuing minor disturbance
N. Windsor Cave	Wet Limestone Forest	18°21'N 77°30'W	230-240m	Diverse, tall, dense, mesophyllic forest within large, relatively undisturbed forested landscape
W. Ecclesdown	Wet Limestone Forest	18°05'N 78°54'W	210-320	Very wet forest at base of undisturbed forested mountains, limestone/shale soils
H. Portland Ridge Upper	Dry Limestone Forest	17°44'N 78°09'W	100-120 m	Undisturbed arid forest; site in a valley where air was more moist, soils deeper, and trees taller than in surrounding areas
K. Portland Ridge Lower	Dry Limestone Forest	17°44'N 78°09'W	80-100 m	Undisturbed arid forest; dense sub-canopy with vines, canopy thin and lacking large trees
O. Hellshire Hills	Dry Limestone Forest	17°51'N 78°12'W	10-20 m	Highly disturbed dry forest, dense thorny shrub layer, grasses in open areas
X. Great Bluff	Dry Limestone Forest	17°52'N 77°45'W	10-30 m	Disturbed very arid forest; canopy sparse, cacti abundant, thorny understory
F. Luana Point West	Thorn Scrub	18°02'N 77°55'W	0-10 m	Heterogeneous grazed thorny thicket with some tall remnant trees
L. Portland Cottage Inland	Thorn Scrub	17°45'N 77°10'W	0-10 m	Homogenous grazed Mimosaceous dry savannah
M. Portland Cottage Seaward	Thorn Scrub	17°45'N 78°10'W	0-10 m	Heterogeneous woodland of dry thorn thicket, dry forest, and coastal woodland
R. Luana Point East	Thorn Scrub	18°02'N 77°54'W	0-10 m	Dense, thorny logwood thickets interspersed with grassy openings

Study Site	Habitat Type	Lat.- Long.	Elevation Range	Site Description
P. Negril	Mangrove	18°11'N 76°43'W	0-10 m	Tall, old/middle-aged diverse mangrove swamp
S. Luana Point	Mangrove	18°02'N 77°54'W	0-10 m	Tall, mature black mangrove swamp in a landscape mosaic with thorn scrub
U. Portland Cottage	Mangrove	17°45'N 78°10'W	0-10 m	Short dense mangrove scrub with shallow open pools
V. Morant Point	Mangrove	18°04'N 78°57'W	0-10 m	Hurricane disturbed dense mangrove scrub thicket
B. Kew Park Oranique	Citrus	18°16'N 77°04'W	290-300 m	Small, little-managed orchard surrounded by pasture, occasional remnant tall wet forest trees
C. Kew Park Orange	Citrus	18°16'N 77°04'W	300-310 m	Small little-managed orchard with small pockets of mesic trees and shrubs
E. Trout Hall	Citrus	18°08'N 77°20'W	220-230 m	Large intensively managed relatively young orchard with many narrow wet ravines
T. Comfort Hall	Citrus	18°10'N 77°34'W	200-210 m	Large, intensively managed orchard with small swampy hollows
D. Kew Park	Shade-coffee	18°16'N 77°04'W	300-310 m	Very young small plantation surrounded by wet forest and pasture; diverse short planted shade trees among several tall remnant forest trees
G. James Hill East	Shade-coffee	18°10'N 77°20'W	610-620 m	Moderately diverse area of plantation; tall, old shade trees of primarily two species, dense coffee understory with a small stream
I. James Hill West	Shade-coffee	18°10'N 77°20'W	610-620 m	Relatively homogenous area of plantation; relatively open understory with abundant banana trees

Study Site	Habitat Type	Lat.- Long.	Elevation Range	Site Description
Q. Baronhall	Shade-coffee	18°13'N 77°22'W	550-560 m	Large, old, homogenous plantation shaded by <i>Inga vera</i> ; wet forest, pasture, and pond near study area
Y. Coleyville	Shade-coffee	18°13'N 77°32'W	630-640 m	Small, young plantation shaded by <i>Inga vera</i> with many banana plants amongst coffee trees
Z. Luana Point West 2	Thorn Scrub	18°02'N 77°55'W	0-10 m	Homogeneous grazed thorny thicket, more closed canopy than site R.

Table 2.—Regression statistics for weight (mg) on length (mm) of Jamaican above ground arthropods.^a

Taxon	n	Length		B ₀ ± 1 SE	B ₁ ± 1 SE	r
		Range (mm)				
Aranae	20	1.1-15.1		-2.077 ± 0.343	2.039 ± 0.235	0.898
Orthoptera & Dictyoptera	32	2.0-19.6		-2.809 ± 0.331	2.125 ± 0.178	0.909
Orthoptera	12	2.2-19.6		-2.649 ± 0.595	2.036 ± 0.308	0.902
Dictyoptera	20	2.0-11.9		-2.974 ± 0.417	2.219 ± 0.229	0.916
Hemiptera	23	1.5-12.8		-3.167 ± 0.294	2.311 ± 0.219	0.917
Homoptera	52	1.1-8.2		-2.453 ± 0.143	1.876 ± 0.119	0.913
Coleoptera	51	1.2-12.1		-2.867 ± 0.226	2.166 ± 0.158	0.890
Lepidoptera	40	2.2-18.6		-3.268 ± 0.255	2.243 ± 0.130	0.942
Diptera	75	1.0-12.5		-2.462 ± 0.196	1.881 ± 0.146	0.833
Nematocera	21	1.0-4.8		-2.562 ± 0.244	1.373 ± 0.207	0.836
Other Diptera	54	1.2-12.5		-2.105 ± 0.178	1.805 ± 0.124	0.895
Hymenoptera	71	1.4-24.3		-3.556 ± 0.183	2.193 ± 0.110	0.923
Formicidae	21	1.6-9.9		-3.730 ± 0.298	2.103 ± 0.238	0.901
Other Hymenoptera	50	1.4-24.3		-3.295 ± 0.241	2.102 ± 0.132	0.917
Total Arthropoda						
Total Insecta (adult)	344	1.0-24.3		-2.842 ± 0.085	2.042 ± 0.055	0.895

^a Equation is Weight in mg = e^{B₀} (length in mm)^{B₁}

Table 3.—Regression statistics for weight (mg) on length (mm) of Jamaican leaf litter arthropods (data are from Strong and Sherry in press).^a

Taxon	n	Length		B ₀ ± 1 SE	B ₁ ± 1 SE	r
		Range (mm)				
Aranae	51	0.8-9.9		-3.197 ± 0.165	2.218 ± 0.122	0.933
Pseudoscorpiones	28	1.0-3.7		-3.742 ± 0.229	2.165 ± 0.232	0.878
"Arthropods" ^{nb}	50	1.5-44.0		-3.831 ± 0.380	2.014 ± 0.183	0.846
Dictyoptera	23	2.4-12.4		-4.289 ± 0.392	2.749 ± 0.232	0.933
Isoptera	75	3.3-5.6		-5.802 ± 0.800	3.177 ± 0.531	0.574
Dermaptera	7	5.8-13.6		-5.647 ± 1.214	2.494 ± 0.540	0.900
Hemiptera	14	2.0-10.5		-3.841 ± 0.263	2.794 ± 0.169	0.979
Coleoptera	75	1.3-14.0		-3.240 ± 0.195	2.513 ± 0.128	0.917
Formicidae	72	1.3-11.5		-4.102 ± 0.132	2.339 ± 0.102	0.939
Holometabolous Larvae	73	1.1-33.5		-5.735 ± 0.370	2.258 ± 0.182	0.827
Total Arthropoda	468	0.8-44.0		-3.257 ± 0.136	1.728 ± 0.084	0.690
Total Insecta	339	1.3-33.5		-3.178 ± 0.197	1.617 ± 0.121	0.589
Total adult Insecta	266	1.3-13.6		-3.893 ± 0.175	2.367 ± 0.117	0.780

^a Equation is Weight in mg = e^{B₀}(length in mm)^{B₁}

^b Includes Diplopoda, Chilopoda, and Isopoda

Table 4.—Slope coefficients (± 95% confidence intervals) of length (mm)-weight (mg) regressions from data collected in Jamaica versus wet and dry sites in Costa Rica^a (above ground arthropods only).

Taxon	Jamaica			Costa Rica, dry forest			Costa Rica, wet forest		
	n	slope	± 95% C.I.	n	slope	± 95% C.I.	n	slope	± 95% C.I.
Orthoptera ^b	32	2.125	0.363	25	1.65	0.47	10	1.96	0.94
Hemiptera	23	2.311	0.453	42	2.48	0.56	16	2.28	0.76
Homoptera	52	1.876	0.239	84	2.65	0.27	62	2.23	0.36
Coleoptera	51	2.166	0.317	150	2.11	0.17	171	1.91	0.19
Lepidoptera	40	2.243	0.263	29	2.50	0.30	7	1.32	1.34
Diptera	75	1.881	0.291	107	1.64	0.24	124	1.59	0.23
Formicidae	21	2.103	0.495	25	2.72	0.51	20	2.31	0.44
Other Hymenoptera	50	2.102	0.265	174	2.07	0.18	122	2.29	0.27
Total	344	2.042	0.108	498	2.16	0.09	535	2.11	0.13

^a Data from Schoener (1980)

^b Includes Dictyoptera

the primary factor determining regression slopes and arthropod shape. One possible explanation for this may be that many above ground arthropods fly to move or escape predators, and may have evolved elongated body shapes for favorable aerodynamics. In contrast, because leaf litter arthropods are primarily runners or walkers, they may be less constrained by aerodynamics, but may benefit from a more compact shape (higher slope) which could be easily maneuvered through leaf litter. In Formicidae and Aranae, which contain few flyers, above ground and leaf litter slopes were similar (overlapping 95% CIs). Conversely, in the other comparable taxa (Dictyoptera, Hemiptera, and Coleoptera), which do contain flyers, the 95% CIs of above ground insects fell below those of leaf litter insects, suggesting that means of locomotion do affect length-weight regression slopes in arthropods.

In conclusion, regression analyses suggested that Jamaican arthropods were relatively thin and light compared to those in drier temperate regions, but were similar to those in other regions of the wet tropics (Table 4). Within Jamaica, arthropods in wetter habitats tended to be long and thin relative to those in drier areas (Figure 2). These results are consistent with the hypothesis that selection has favored elongated body shapes in wet regions and habitats where arthropods are little constrained by desiccation. However, leaf litter arthropods, which are probably protected from desiccation, were relatively compact compared to those collected above ground, suggesting that other constraints, perhaps those imposed by means of locomotion, also affect arthropod shape.

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